

Ultraviolet reflection of berries attracts foraging birds. A laboratory study with redwings (*Turdus iliacus*) and bilberries (*Vaccinium myrtillus*)

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Unlike humans, birds perceive ultraviolet (UV) light (320–400 nm), a waveband which is known to play a role in avian mate choice. However, less attention has been paid to the role of UV light in avian foraging. Some blue, violet and black berries reflect UV light. The colour of berries might be an effective advertisement for avian seed dispersers and indicate the stage of fruit ripeness. We conducted an experiment to test how the UV reflection of berries affects birds' foraging. Redwings were allowed to choose between UV-reflecting bilberries and rubbed bilberries (UV reduced) in the presence and absence of UV light. We used wild-caught adult and hand-raised juvenile birds to assess possible differences between experienced and naive birds. We found that adult redwings preferred UV-reflecting berries when UV illumination was present, but when UV illumination was absent, they did not distinguish between the two berry types. Our study therefore shows, for the first time, that UV wavelengths are used when birds feed on fruit. However, naive birds showed no preferences, suggesting that age and/or learning may affect frugivore preference for UV reflectance.

Keywords: ultraviolet; foraging; redwing; bilberry; plant–animal interactions

1. INTRODUCTION

The ecological and evolutionary interactions between frugivorous animals and their fruiting plants have been of interest for a long time. The bright and conspicuous colours of fruits attract frugivorous birds and such fruits are visible for a considerable distance against a background of green foliage (Ridley 1930). In their review article, Willson & Whelan (1990) examined several hypotheses for the evolution of fruit colours. Most of them are based on adaptation to dispersal, defence or physiological requirements. Their hypotheses on adaptation for avian foraging suggest that (i) birds prefer fruits of certain colours, (ii) certain colours have been selected because of their conspicuousness to their foragers, (iii) colour indicates fruit maturity, (iv) colours facilitate quick recognition of food sources particularly in migrant birds, and (v) nutritionally poor fruits mimic nutritionally rich fruits. They also suggested that social learning (e.g. young birds mimic their parents when foraging), sampling behaviour and hunger-driven consumption could affect their choice. According to them, additional tests with birds of different ages and experience would provide some new information on their preferences.

Diurnal birds see the world in a different way to humans. Their ability to see is based on at least four kinds of photopigments in the cone cells of the eye's retina

(range 320–700 nm; tetrachromatic colour vision including near-ultraviolet (UV) wavelengths of 320–400 nm) instead of humans' three types of photopigments and trichromatic colour vision system of 400–700 nm. Bennett & Cuthill (1994) suggested that birds can use their UV vision, e.g. in signalling, foraging and orientating. The significance of UV light in mate choice and sex recognition has been demonstrated in many laboratory experiments in recent years (see Bennett *et al.* 1996, 1997; Hunt *et al.* 1997, 1998; Andersson *et al.* 1998; Cuthill *et al.* 1999) and in the field (Johnsen *et al.* 1998). Viitala *et al.* (1995) were the first to show that kestrels (*Falco tinnunculus*) locate potential prey sites on the basis of vole scent marks which are visible in UV light. It has also been demonstrated that blue tits (*Parus caeruleus*) use UV cues to detect cryptic prey (Church *et al.* 1998). However, experimental studies concerning UV light and bird foraging are still scarce.

Burkhardt (1982) showed by photographing that many blue and violet berries with a waxy bloom reflect in UV light and suggested that this might be related to foraging in birds. He also noticed that 'rubbing off the bloom results in a dramatic decrease of the UV reflectance' (Burkhardt 1982, p. 156). Willson & Whelan (1989) tested the importance of a wax layer in the preferences of birds using UV-reflecting and non-reflecting berries of the same species. Experiments were conducted both in the field (fruit removal test) and in an outdoor aviary (tests of preference). They removed the wax layer by rubbing or passing the berries quickly through a flame. However,

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they did not observe any difference in preference between waxy and waxless berries. They suggested that frugivorous birds might not possess functional vision at UV wavelengths and that the signal character of the bloom is context dependent.

The fruit colour preferences of birds have been studied in many experiments particularly in the field (see e.g. Gervais *et al.* 1999), but also in the laboratory (e.g. McPherson 1988). However, so far the significance of light conditions and birds' ability to see in UV light have been ignored (but see Willson & Whelan 1989).

In this study, we were interested in the significance of UV light in plant-animal interactions, particularly in the foraging behaviour of birds. We tested (i) whether birds prefer UV-reflecting bilberries (*Vaccinium myrtillus*) over rubbed (UV-reduced) ones, and (ii) whether there are any differences in preferences between adults, which are expected to be familiar with berries, and naive juvenile birds, which have not yet come across any type of berry. A difference between experienced and naive birds would suggest that learning plays a role when preferences are developing. The experiment was carried out under controlled laboratory conditions.

2. MATERIAL AND METHODS

(a) *Experimental place and subjects*

The experiment was conducted at Konnevesi Research Station (63°37'N, 26°21'E), central Finland in late August–September 1998. We used redwings (*Turdus iliacus*), which are abundant frugivorous thrushes nesting in Finland. In late summertime, bilberries are a common part of the diet for redwings. Birds were captured and kept with the permission of the regional environment centres (Central Finland Regional Environment Centre, permission LS-11/98 and North Savo Regional Environment Centre, permission 0698L0267–254).

During June and at the beginning of July 1998, we mist-netted adult birds. Their nest and brood (chicks *ca.* 9–12 days old) were also taken. The birds were fed with a food mixture containing minced meat, cottage cheese, salad, bread, dog food, apple, egg and extra vitamin and calcium (a recipe from Helsinki Zoo, Finland) and with mealworms (*Tenebrio molitor*). Water was available *ad libitum*. Parent birds started to feed their chicks in captivity but chicks were also fed if necessary. We kept the birds in indoor cages (1.2 m × 0.55 m × 0.60 m), first with one brood in one cage and then one to four individuals per cage under a natural photoperiod of 14 L:10 D. The housing room had four large windows and additional fluorescence tubes. After the experiment in September 1998 we released the birds back to nature.

(b) *Experimental cage and habituation*

We performed the experiment in an indoor cage (0.64 m × 0.69 m × 0.71 m). The illumination for the cage was provided by an Osram Eversun L 40W/79K solarium tube (emitting mainly between 300 and 400 nm) and an Osram Biolux L 18W/72 tube (emitting mostly in visible wavelengths of 400–700 nm). We offered berries to birds in the presence of UV light and in visible light without UV light. Either a UV-blocking or UV-transmitting filter was used to obtain the illumination needed (figure 1a). We measured reflectance spectra with a calibrated spectroradiometer (EG & G Gamma Scientific GS 3100 with an EG & G RS-22UV xenon fibre optic light

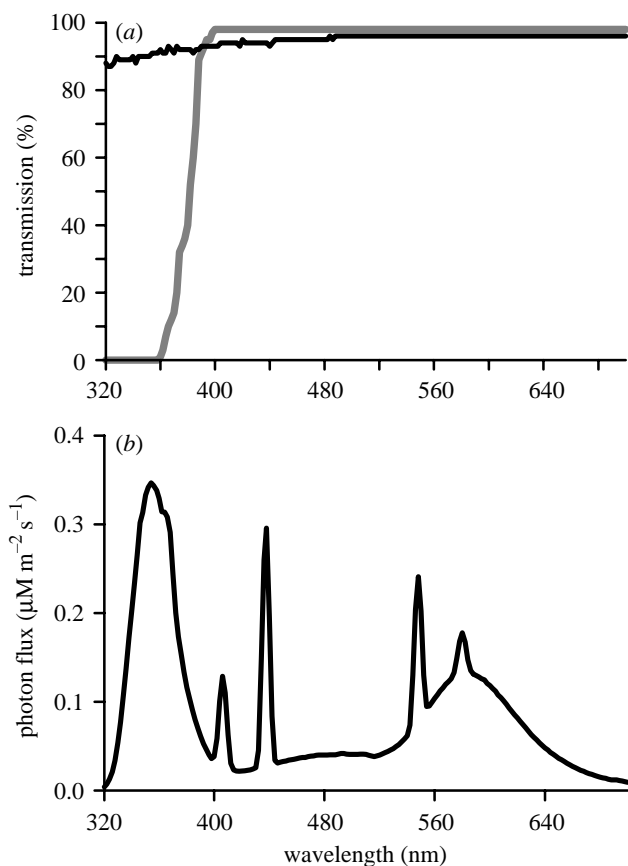


Figure 1. (a) Light transmissions in the experiment with a UV-transmitting filter (black line) and a UV-blocking filter (grey line). (b) Illumination in the experimental cage with two tubes without filters. All measurements were recorded in the experimental cage.

source). When measuring illuminations in the experimental cages, a miniature cosinus receptor (EG&G 700–8D, 250–1700 nm) was used in the spectroradiometer without a standard light source. The cosinus diffusor was inclined *ca.* 15° towards the tubes at a distance of 0.60 m (at the same position where the berries were placed on a tray in the cage). The spectra were recorded at 2 nm intervals between 320 and 700 nm and were measured relative to a LabSphere™ 98% reflectance standard. However, animal photoreceptors respond to photons independent of energy and the light intensity of illumination was measured as energy flux per unit area ($E(\lambda)$, W m^{-2}) rather than photon flux. Therefore, we transformed the units of the spectrum from radiance to irradiance so as to be able to recalculate the light intensity in photon flux ($Q(\lambda)$, $\text{mM m}^{-2} \text{s}^{-1}$) by following the formula $Q(\lambda) = 0.0083519\lambda E(\lambda)$ (Endler 1990). The illumination of the cage is shown in figure 1b. The experimental cage was painted with a matt black with a very low reflectance in all wavelengths of light and the bird had one perch and water always available.

We randomly selected 20 naive chicks from the broods for the experiment. The chicks were tested at the age of approximately two months and could easily feed by themselves. All adult birds were used ($n = 9$; four females, four males and one unsexed). We habituated the birds to eating mealworms in the experimental cages before starting the experiment so that the birds were familiar with the cages. Before each trial, the birds were in the experimental cages for *ca.* 2 h without food so that they were motivated to eat.

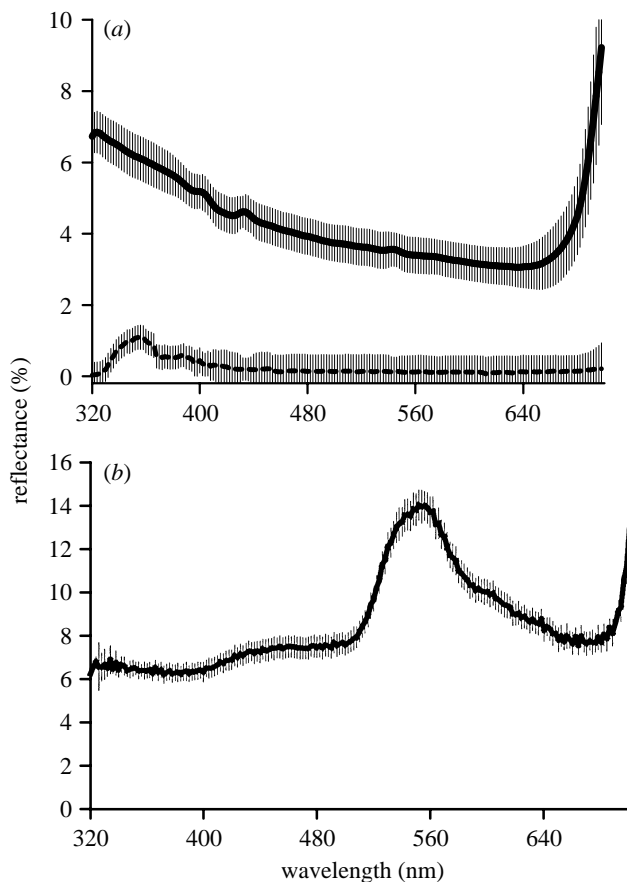


Figure 2. Mean reflectance spectrum (\pm s.e.) of (a) intact ($n=15$, solid line) and rubbed ($n=15$, dashed line) bilberries and (b) 15 leaves of alder. The spot area measured was $1\text{ mm} \times 1.5\text{ mm}$. Notice that the relative reflectance of the berries compared to the leaves might be higher because, in the measurements, the amount of light coming into contact with the berry surface is smaller (round shape of berry) than the amount of light coming into contact with the leaf surfaces (flat surface).

(c) Experiment and statistical analyses of results

In the experiment the bird could choose between UV-reflecting bilberries and manipulated bilberries (UV reduced), once in UV+ (UV present) and once in UV− (UV absent) light conditions (figure 1a). The reflecting wax layer was removed by rubbing the wax off by hand (rubbed berries, which are black and more shiny to the human eye versus intact berries, which are bluish to the human eye; figure 2a). By doing this we had berries with the same taste and shape but different colours. Through our preliminary feeding trials in 1997, we observed that birds readily eat rubbed berries (H. Siitari, personal observation) and Willson & Whelan (1989) also noted this. There is also a natural form of bilberry that lacks the wax layer and appears like our rubbed berries. However, to avoid possible differences in natural waxy and waxless berries we used only rubbed berries as non-reflecting ones in our trials. The texture of the rubbed berry did not appear to be affected by rubbing.

We measured the reflectance spectra of 15 bilberries with the spectroradiometer to assess the colour differences in intact and rubbed berries. A standard light source (the xenon lamp) was used at an angle of 45° to the upper surface of the measuring berry. Again, spectra were recorded at 2 nm intervals between 320 and 700 nm at an angle of 45° to the normal and measured relative to a reflectance standard. The spot area measured was

$1\text{ mm} \times 1.5\text{ mm}$. For details of the measurement system see § 2(b). After the first measurement we rubbed the wax off and measured the spectrum again. Thus, each berry was measured twice, first with a wax layer and then without it. The mean reflectance spectra of the 15 intact and rubbed berries are shown in figure 2a.

We offered berries to the birds on a black tray ($0.08\text{ m} \times 0.45\text{ m}$) covered with green, grey alder (*Alnus incana*) leaves (reflectance spectrum in figure 2b). For the most natural contrast it would have been best to use bilberry leaves. However, these small leaves dried rapidly and their colour changed from green to brown. We placed eight berries (four intact and four rubbed ones) in a row in randomized order. The arrangement of the trial per individual (UV+ or UV−) was randomized to avoid the effects of learning on the results. For each bird, trials were performed on separate days. Because the size of the berry could affect choice, only berries of similar size were used in each trial.

We observed the birds through a small window during the trials. Each trial was terminated after the bird had consumed half the berries (in this case four bilberries). Since the choosing order of the berries might reflect the preferences of the birds we ranked the berry choices in the same order that the bird took the berries. The first choice obtained a score of four, the second a score of three, the third a score of two and the last a score of one. Thus, the sum of the scores was ten in each trial. The age classes of the redwings were analysed separately. We compared the scores of intact berries eaten in two different illuminations using repeated measures ANOVA (within factor, 'light' with two levels: UV+ and UV−). A paired samples *t*-test was conducted for the data comparing the ranking scores of intact and rubbed berries in the two different illuminations, respectively. All statistical tests were two-tailed and conducted with the SPSS 8.0 for Windows program on \log_{10} -transformed data.

3. RESULTS

(a) Adult birds

The adult redwings showed a clear preference for intact bilberries over the rubbed ones in the UV+ trial (paired samples *t*-test, UV-transmitting filter $t_8 = -3.91$ and $p = 0.013$), but did not prefer either berry colour type in the UV− trial ($t_8 = 0.577$ and $p = 0.58$) (figure 3a). There was also a difference between the scores given for intact berries in the UV+ and UV− trials (RMANOVA $F_{1,8} = 10.8$ and $p = 0.011$).

(b) Naive birds

In the naive birds, no difference was found between the intact and rubbed berries in either the UV+ or UV− trials (paired samples *t*-test, UV-transmitting filter $t_{19} = 1.23$ and $p = 0.23$ and UV blocking filter $t_{19} = 0.79$ and $p = 0.44$) (figure 3b). Similarly, no difference was found between the scores given for intact berries in the different trials (UV+ or UV−) (RMANOVA $F_{1,19} = 0.042$ and $p = 0.839$).

4. DISCUSSION

Our results indicate that the waxy berries of bilberry which reflect UV light might be a good advertisement for adult redwings in certain light environments. The effect of UV light reflecting the wax layer was well demonstrated

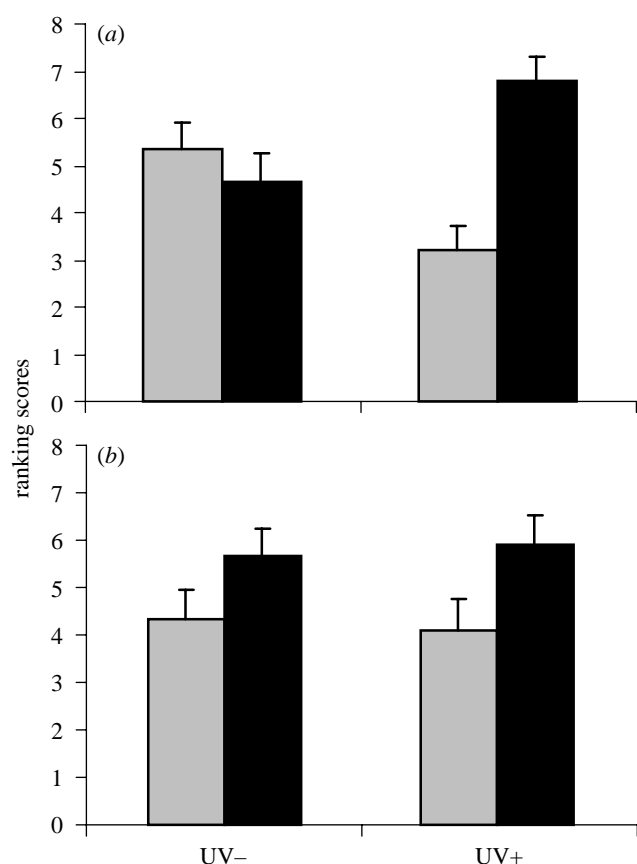


Figure 3. Mean ranking scores for (a) adults and (b) chicks in the two different illuminations (UV- or UV+). Grey bars indicate the mean scores given for the rubbed berries chosen and black bars indicate the mean scores given for the intact berries chosen. The maximum score was ten. Error bars represent the standard errors calculated over individual means. For the statistics see § 3.

since the preferences of adults altered depending on the filter used (UV+ or UV- light conditions). In accordance with these findings there was also a difference between the order in which birds took the intact berries in the presence or absence of UV light; intact berries were chosen first when UV light was present but such discrimination was not detected when UV light was absent (figure 3a). Thus, the UV-blocking filter acts as a control treatment and implies that it is the UV light that affects the birds' choice. The behaviour of the adult birds in the experimental cages was quite similar in both trials. However, they tended to be less active during the UV- trial compared to the UV+ trial, although they readily ate half the berries in both trials.

Such an effect of the UV-reflecting wax layer was not found among naive juveniles in either the UV+ or UV- trials. As the ranking scores in figure 3b show, young birds tended to choose the intact berry first in both trials, but the difference between the scores was not significant in either the UV+ or UV- trials. This lack of preference could be explained, for example by the sampling behaviour of the naive birds. Juveniles might also learn what to eat by mimicking adults (i.e. by social learning). In addition, individual learning could affect food preferences. Redwings feed their chicks after they have left the nest and naive birds follow their parents in a flock

searching for food. One possible explanation is the difference in sensory capacity between young and adult birds and this might be worth testing in future experiments. No difference in behaviour between the trials was observed in naive birds.

Birds disperse seeds of many plant species. Some fruit colours may attract birds more than others (Ridley 1930). If a fruit colour is easily recognized and associated with food, it might function as an efficient advertisement for seed dispersers. According to Willson & Whelan (1990) red and black are most common fruit colours of bird-dispersed fruits in the world, but in boreal regions the amount of blue or ultraviolet fruits is also high. The fact that many blue or black fruits reflect in UV, even without a wax layer, has also been ignored (Willson & Whelan 1989; J. Viitala, unpublished data). It is the wax layer that reflects UV light in bilberries and gives a 'colour' to the berry. When it was rubbed off, the colour of the berry changed from ultraviolet to almost black. One ultimate function of the wax layer might be protection against micro-organisms and diminishing water exchange (Burkhardt 1982). It can also protect the berry from deleterious wavelengths of sunlight. However, a selective advantage of the wax layer might be that it serves as a good advertisement for avian seed dispersers that are sensitive to ultraviolet light.

In nature, bilberries grow in habitats similar to 'woodland shade' (classification in Endler (1993)) which means natural light environments rich in short wavelengths. Thus, in woodland shade environments signal colours should be blue, blue-green or, perhaps, ultraviolet to maximize their brightness (Endler 1993). In our experimental light environment, the amount of UV light was relatively high compared to other parts of the light spectrum, such as in woodland shade. Thus, the brightness of intact berries should be high when UV light is present, as in our UV+ light conditions. One can criticize this because the amount of UV light was higher than in natural conditions, but in this case we altered the light conditions particularly to find out the significance of UV light. If this experiment had been done in the field it would have been important to use the natural light environment of the fruiting plant. This might be one explanation why Willson & Whelan (1989) obtained contrary results. Little is indicated about the light environment used in their experiment. Moreover, different effects may be observed in different species; indeed, this may be one reason for the difference in the conclusions between their experiment and this one. Whelan & Willson (1994) demonstrated that the environmental context of fruit presentation may have strong effects on the fruit preferences of migrating birds, i.e. highly accessible fruits are preferred over the less accessible ones.

Over 30 diurnal bird species have been suggested to have a visual system based on four 'main' colours including UV (see the review in Bennett & Cuthill 1994). Physiological studies (e.g. Maier & Bowmaker 1993; Bowmaker *et al.* 1997; Hart *et al.* 1998) have demonstrated that many passerine birds, including some thrushes (Chen *et al.* 1984), have receptors sensitive to UV light. Diurnal birds may be even more sensitive to UV wavelengths compared to other wavelengths (Kreithen & Eisner 1978; Burkhardt & Maier 1989; Church *et al.* 1998). Thus, the significance of UV

light as an information channel for birds, which is invisible to humans, needs more behavioural and observational research.

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